Regulation of Predator-Prey Systems through Spatial Interactions: A Possible Solution to the Paradox of Enrichment

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Many natural predator-prey systems oscillate but persist with densities staying well away from zero. Non-spatial predator-prey models predict that in environments where prey on itself can do well, a predator-prey system can oscillate with troughs in which the populations become vanishingly small. This phenomenon has become known as the paradox of enrichment. In this paper the role of space in bounding overall population oscillations is analysed in the simplest version of spatial predator-prey models: a two-patch model for a Lotka-Volterra system and a Rosenzweig-MacArthur system with logistic prey growth and Holling type II functional response of predator to prey density within each patch. It was found that the spatial interactions can bound the fluctuations of the predator-prey system and regulate predator and prey populations, even in the absence of density dependent processes. The spatial dynamics take the form of locally asynchronous fluctuations. Enrichment of the environment in a two-patch model does not necessarily have the paradoxical consequence that the populations reach densities where extinction is likely to occur.

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Many natural predator and prey populations persist while their densities show sustained oscillations. Hence these populations must be regulated in such a way that the densities are kept away from the values where extinction is likely to occur. In contrast to this, predator-prey systems that are kept in the laboratory tend to show fluctuations in densities that are severe enough to drive them to extinction (Gause 1934, Huffaker 1958, Huffaker et al. 1963).

Rosenzweig-MacArthur models for predator-prey systems can produce dynamics where densities show bounded fluctuations around an unstable equilibrium point. Only the amplitude of the fluctuations changes rapidly with the models parameters. The parameter region where predator-prey models allow oscillations with a relatively small amplitude is very restricted. For instance, the amplitude increases with carrying capacity of the prey population. For large carrying capacities the densities can reach values where natural populations would certainly go extinct. Enrichment of the environment for the prey species thus makes life for prey worse, not better. This has become known as the paradox of enrichment (Rosenzweig 1971).

Predator-prey models offer a good description of the changes in numbers of laboratory predator and prey populations (Maly 1969). It is rather unlikely though, that such models faithfully describe natural predator and prey populations because one would then be forced to assume that these are described by parameters only coming from the narrow range where oscillations with a small amplitude are possible. Therefore, natural predator-prey systems must be regulated through a mechanism that is not described in the Rosenzweig-MacArthur predator-prey models. Since the amount of space that laboratory populations live in is small compared to those of natural populations, one is readily led to the hypothe-

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sis that spatial interactions must contribute to the regulation of natural predator-prey systems.

In this paper I investigate how and when spatial interactions can regulate predator prey populations using simple models for spatial predator-prey systems. Others have addressed this question before using verbal arguments (Nicholson and Bailey 1935, Den Boer 1968) and model studies. Models for spatial predator-prey systems date back to the 1970's. Spatial versions of the Lotka-Volterra model were formulated by Comins and Blatt (1974) and Steele (1974). Recently Hassell et al. (1991) and Comins et al. (1992) showed that models for host-parasitoid systems can persist on a large grid, where the non-spatial models drive themselves to extinction. This also holds for a two-patch host-parasitoid system (Adler 1993). Most of these models are discrete in time and therefore are more appropriate for host-parasitoid interaction. De Roos et al. (1991) and Wilson et al. (1993) demonstrated the stabilising influence of a diffusion limited predator-prey interaction.

Simulation models have the disadvantage that important aspects of the dynamics may be missed. Therefore I will apply recently developed methods for automated bifurcation analysis (Khibnik et al. 1993). These make a detailed description of the behaviour of a dynamical system possible and can reveal qualitative behaviour that is easily overlooked when one is limited to simulations alone.

Two-patch models

The models I will analyse here are the simplest spatial models possible. They describe a predator-prey system with two identical compartments. Individuals move between the two compartments with a constant probability per unit of time. Such models allow for two different sorts of interpretations. The two patches can be viewed either as a predator-prey metapopulation consisting of two local populations coupled through migration, or a predator-prey system living in a space discretised in the two compartments. Whenever spatial effects occur in a two-compartment system, they can be expected to occur as well for finer discretisations. Two-patch models thus give an insight in how and when spatial interactions can influence population densities.

Because the patches are identical the densities in both patches can be equal. When this is the case the densities of course stay equal for ever after and the population densities behave as in the non-spatial case. These solutions are symmetrical solutions because patches behave exactly the same. To identify the effect caused by spatial interactions the stability of symmetrical solutions is studied. A symmetrical solution is stable when it is stable in the non-spatial case *and* when small differences between the patches disappear instead of amplify.

The models in this paper are very simple forms of metapopulation models. It is often argued that metapopulations fluctuate less than a single well mixed population because the local populations will fluctuate out of synchrony and therefore dampen the fluctuations in the densities of the population as a whole. A bit of a weak point in this reasoning is that it is not always clear why the local populations in a metapopulation should fluctuate asynchronously. In the models presented here the densities of the local populations can fluctuate in synchrony in the symmetrical solutions. Whenever asynchronous fluctuations are an intrinsic property of predator and prey populations in a patchy habitat they should emerge in the form of long lasting non-symmetrical solutions in the model.

A two-patch Lotka-Volterra model

The classic Lotka-Volterra model is based on the assumptions that the prey density grows exponentially in the absence of predators and that the predator density decays exponentially in the absence of prey. The contact rate of prey and predator is linear. For a two-patch version of the Lotka-Volterra model the additional assumption has to be made that the prey and predators react to local densities, i.e. the densities in their patch, only. The patches are coupled through migrating individuals. The model given here is a special case of the model formulated by Comins and Blatt (1974). The equations read as follows:

$$\begin{aligned}
\frac{dN_1}{dt} &= rN_1 - N_1P_1 + d_n(N_2 - N_1) \\
\frac{dP_1}{dt} &= N_1P_1 - \mu P_1 + d_p(P_2 - P_1) \\
\frac{dN_2}{dt} &= rN_2 - N_2P_2 + d_n(N_1 - N_2) \\
\frac{dP_2}{dt} &= N_2P_2 - \mu P_2 + d_p(P_1 - P_2)
\end{aligned} \tag{1}$$

where N_i and P_i denote the density of, respectively, the prey and the predator in patch i. The constant r is the growth rate of the prey population in absence of predators and μ the death rate of predators. The contact rate between prey and predators is set to unity by a scaling of the densities. The migration rate of the prey is given by d_n and that of the predator by d_p. Every individual has a constant probability of leaving. The net effect of, for instance, prey migration in patch one then is $d_n(N_2-N_1)$. Note that if $N_1 = N_2$ and $P_1 = P_2$ the migration terms are zero and the populations in both patches obey equal rates of change, hence the densities will stay equal.

It is well known that the solutions of models in which the spatial domain is continuous (instead of being discrete as it is in this paper) and in which the local interactions are given by the Lotka-Volterra model, are asymptotically spatially uniform. Spatial variation decreases over time and in the end every solution becomes spatially homogeneous (Murray 1975). The densities change over time but will behave like a stiff board moving up and down. The two-patch Lotka-Volterra model can be seen as a discretisation of such a model. Not surprisingly it has a similar property: for all solutions of system (1) with positive initial conditions and at least one positive migration rate, any differences between the patches will eventually disappear (Jansen 1994a).

When the densities in both patches are equal the densities oscillate in synchrony around an equilibrium value, exactly as in the non-spatial Lotka-Volterra model. Since there exist no long lasting non-symmetrical solutions, what remains to be assessed is the stability of the symmetrical solutions. This might seem a superfluous exercise since if all orbits converge towards symmetrical solutions there obviously must exist symmetrical solutions which attract. The point is though, that some of the symmetrical solutions can be unstable and will not appear in long term dynamics.

The non-spatial Lotka-Volterra model has a neutrally stable equilibrium point, surrounded by neutrally stable closed orbits. A neutrally stable closed orbit is an orbit to which nearby orbits always stay close without having to converge to it. Small perturbations from such a closed orbit need neither disappear nor amplify and can thus induce a small change in the amplitude of the orbit.

In the spatial Lotka-Volterra model the symmetrical equilibrium point is the only possible positive equilibrium. It is always neutrally stable, just as in the non-spatial Lotka-Volterra model (Nisbet et al. 1992). Symmetrical closed orbits with a small amplitude, i.e. orbits close to the equilibrium, are neutrally stable as well. For the two-patch Lotka-Volterra model neutral stability means in particular that when *small* differences in densities between the patches are introduced they will disappear but that they might induce small changes the amplitude of the symmetrical closed orbit. Not all closed orbits need to be neutrally stable: those with small amplitude are but larger ones can be unstable. Then, *small* differences in density between the patches will amplify and cause large changes in amplitude. Hence almost all orbits starting close to an unstable symmetrical closed orbit grow away from it.

As seen above, every solution eventually must lose all differences in densities and thus every orbit eventually must approach a (neutrally stable) symmetrical orbit. Therefore system (1) must have orbits that form connections between large unstable orbits and neutrally stable orbits. Fig. 1 shows a solution with a part of one such connecting orbit. It starts with very little differences in densities between the patches and fluctuations with a large amplitude. The differences then get larger from oscillation to oscillation and the amplitude decreases. Finally the differences disappear as the orbit runs into a symmetrical closed orbit with a small amplitude.

Large amplitude orbits do not become unstable for all combinations of the migration rates. What is typically needed is little or no prey migration and intermediate predator migration. This gives a hint to the mechanism that underlies this instability. During a part of a large oscillation the predator densities are very low. The prey density then grows almost exponentially. With little or no prey migration, a small difference in prey density also grows exponentially. After the prey densities have built up, the predator density increases, causing a subsequent decrease in prey density. The patch that initially had more prey will produce more predators. The increase in predator density is fast and hence migration will have little impact. After the prey density has dropped the predators will die off exponentially. The difference in predator densities will decrease during this phase due to predator migration and mortality. However, the difference in predator densities will now cause differences in prey densities between the patches. For very low values of predator migration the differences between initial prey densities will not be carried over from one patch to the other and for very high predator migration rates the difference in predator densities will disappear very fast so that the predator densities in both patches are practically the same. For intermediate values

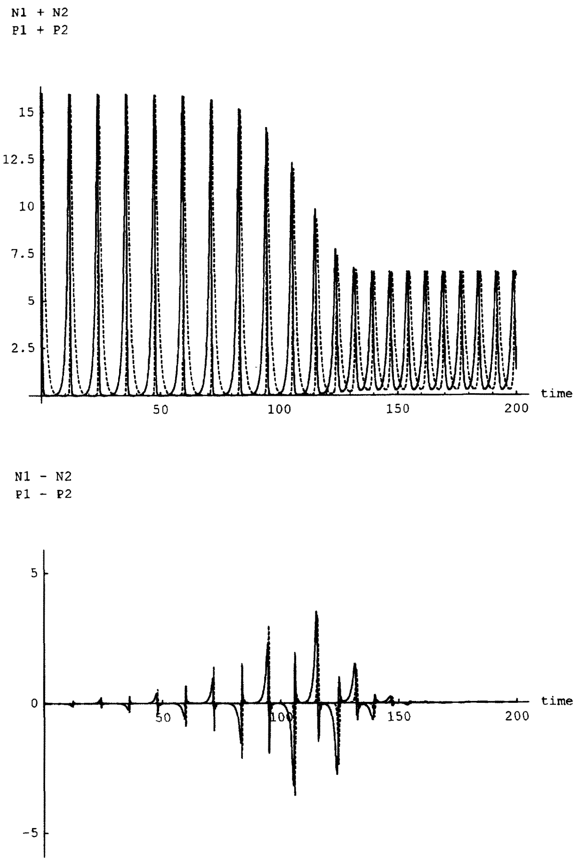

Fig. 1. The total prey (solid line) and predator (dashed line) densities in two patches, $N_1 + N_2$ and $P_1 + P_2$ (upper), and the differences between the densities in the patches of prey (drawn line) and predator (dashed line), $N_1 - N_2$ and $P_1 - P_2$ (lower), versus time for a solution of system (1) with $r = 1, \mu = 1, d_n = 0, d_p = 0.7$.

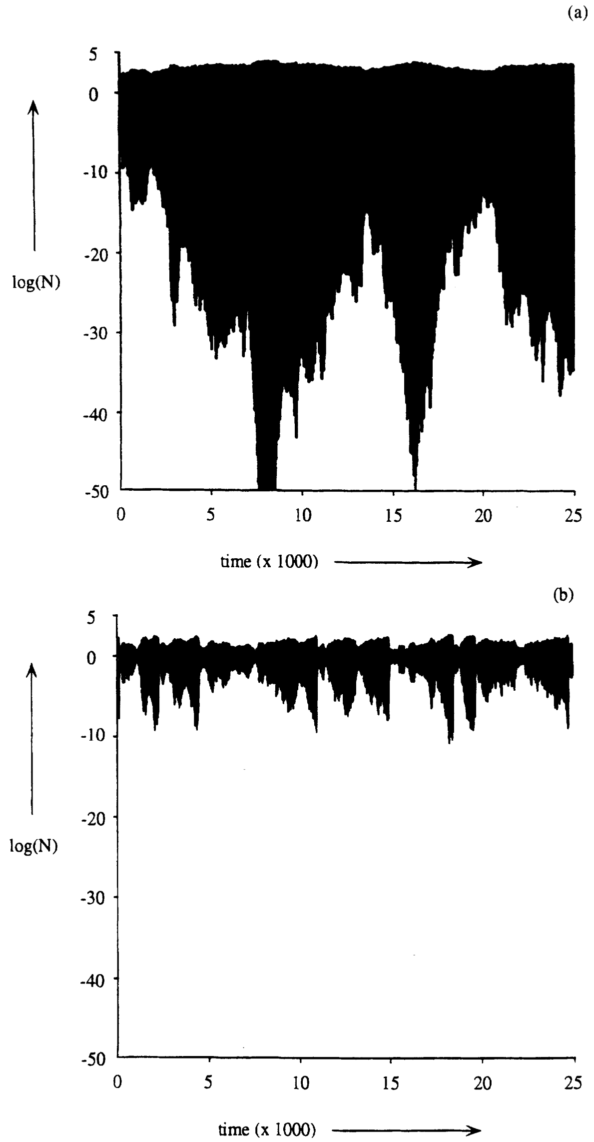

Fig. 2. (a) The logarithm of the average prey densities versus time, for a solution of a non-spatial Lotka-Volterra model with noise on the predator death rate. The solutions show unbounded drift and attain very low densities. (b) The logarithm of the average prey densities over the two patches versus time for a solution of system (1) with noise on the predator death rate μ. The parameters and the noise are chosen identical to those used for Fig. 2a. The noise was applied such that the predator death rate was distributed uniformly over 1 ± 0.1 but that the two patches experience identical predator death rates at any time. Although the densities still drift they do not reach the extremely low densities that occur frequently in the non-spatial Lotka-Volterra model. Parameter values $r = 1$, $\mu = 1$, $d_n = 0$, $d_p = 0.7$.

of predator migration, however, the difference in prey densities between the patches can increase from oscillation to oscillation. This is supported by the fact that an increase in the predator death rate, μ (which shortens the period over which substantial predator migration takes place), enlarges the region where unstable symmetrical orbits are possible (Jansen 1994a).

The Lotka-Volterra model has often been discarded as a good model for ecological interactions since it is structurally unstable. Small changes in the model qualitatively alter its behaviour. Environmental noise, for instance, causes the solutions to "drift" away from any orbit, bringing the densities sooner or later to values where extinction is more than likely (Fig. 2a). For the two-patch Lotka-Volterra this is not the case. The closed symmetrical orbits are identical to those of the non-spatial model and will not persist (in the sense that although they will only change slightly they will not remain closed) and change into an orbit on which the densities drift from high to low values. The orbits that connect large symmetrical orbits to small symmetrical orbits are structurally stable and do persist; they will undergo some slight changes as well but will still form a connection between symmetrical orbits with high and low amplitudes. This makes that the two-patch Lotka-Volterra model reacts very differently to environmental noise from the non-spatial Lotka-Volterra model.

Fig. 2b shows the dynamics of a perturbed two-patch Lotka-Volterra model in which the predator death rate at any moment is the same in both patches, but fluctuates randomly over time. As in the non-spatial model (Fig. 2a) the noise causes drift in the amplitude. However, when the fluctuations become very large and some differences in densities between the patches still exist, the mechanism at work in Fig. 1 starts to operate. The differences between the patches induce reductions in the amplitude from time to time. The densities in the spatial Lotka-Volterra model therefore rarely reach extremely low values.

A classical predator-prey model in two patches

The two-patch variant of a classical Rosenzweig-MacArthur predator-prey model can be derived by replacing the exponential prey growth function with logistic growth and the functional response with a Holling type II functional response in system (1). This gives the following equations:

$$
\begin{aligned}
\frac{dN_1}{dt} &= rN_1\left(1-\frac{N_1}{c}\right)-\frac{bN_1P_1}{1+N_1}+d_n(N_2-N_1)\\
\frac{dP_1}{dt} &= \frac{bN_1P_1}{1+N_1}-\mu P_1+d_p(P_2-P_1)\\
\frac{dN_2}{dt} &= rN_2\left(1-\frac{N_2}{c}\right)-\frac{bN_2P_2}{1+N_2}+d_n(N_1-N_2)\\
\frac{dP_2}{dt} &= \frac{bN_2P_2}{1+N_2}-\mu P_1+d_p(P_1-P_2)
\end{aligned}
\qquad (2)
$$

Here c is the prey's carrying capacity and b the saturation value of the functional response. The scaling chosen is such that the encounter rates and conversion coefficiency are scaled out but that the carrying capacity is preserved as a parameter.

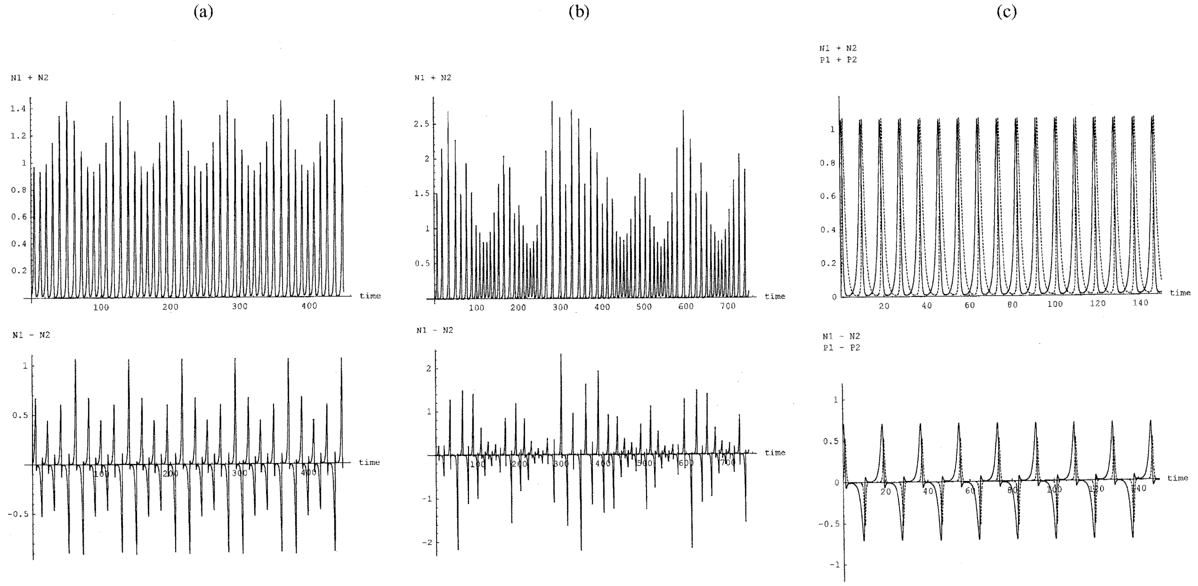

Fig. 3. The total prey densities over the two patches (upper) and the difference in prey densities (lower) versus time for various solutions of system 2. (a) A quasi periodic solution with $r = 1$, $c = 7$, $d_n = 0$, $d_p = 0.7$, $b = 9.96$, $\mu = 1$. (b) A "chaotic" solution with $r = 1$, $c = 5$, $d_n = 0$, $d_p = 0.6$, $b = 9.96$, $\mu = 1$. (c) A periodic solution with $r = 1$, $c = 20$, $d_n = 0$, $d_p = 0.7$, $b = 9.96$, $\mu = 1$ (the dashed lines represent total predator densities and difference in predator densities)

For the non-spatial model a Hopf bifurcation takes place for $c = \frac{b+\mu}{b-\mu}$; it has a stable equilibrium for $c < \frac{b+\mu}{b-\mu}$ and a stable limit cycle for $c > \frac{b+\mu}{b-\mu}$. The symmetrical solutions of this model are identical to those of the non-spatial model but can have different stability properties. The symmetrical limit cycle, for instance, can become unstable for certain parameter combinations, typically when the prey migration is low and the predator migration rate has an intermediate value (*c.f.* system (1)).

The major difference between the dynamics of models (1) and (2) is that the latter exhibits long-term dynamics while differential densities between patches persist. The orbits end up on an attractor which is not symmetrical. Clearly, a non-symmetrical attractor must exist when the symmetrical limit cycle is unstable. However, a non-symmetrical attractor can also occur when the symmetrical limit cycle is stable. It typically exists in and around the region where the symmetrical limit cycle can be unstable.

The dynamics on some of the non-symmetrical attractors is depicted in Fig. 3. When there are small differences in densities the fluctuations grow in amplitude. When the fluctuations have considerable amplitude the differences start to increase which dampens the fluctuations. The dynamics can be quasi-periodic (Fig. 3a), "chaotic" (Fig. 3b) or periodic (Fig. 3c). Notice that the differences in densities change sign with every next peak in the average densities. In terms of density in a patch it means that a large peak is followed by a smaller peak. The other patch shows a similar but out of phase pattern, i.e. a small peak when the other patch has a large peak. Thus long term average population densities in both patches will be approximately the same.

On the paradox of enrichment

Richness in dynamical behaviour can be a delight to the mathematician and a nightmare to the ecologist. For the latter the mathematical trees probably only obscure the view of the forest. I will therefore not present a stability analysis of the different solutions but concentrate on an ecologically important feature of the model. Interested readers can find a detailed numerical bifurcation analysis of system (2) in Jansen (1994b).

The ecological relevance of these models lies first and foremost in the fact that the fluctuations in the average densities are often less extreme than in the non-spatial models. This is due to the fact that spatial models allow for non-symmetrical solutions. When the peaks and troughs in densities do not coincide the amplitudes of the fluctuations in the average densities are reduced. This means that populations in a two-patch system are less likely to go extinct than they would in a single patch.

I will demonstrate this by investigating the dependence of the amplitude of the fluctuations in model (2) on the carrying capacity. In the non-spatial analogue of model (2) the amplitude increases rapidly with carrying capacity. Fig. 4a shows the minima and maxima of the logarithmic prey density of the non-spatial variant of system (2), which is identical to the symmetrical solution of (2). For small carrying capacities the equilibrium is stable and the minima and maxima coincide. For increasing carrying capacity the equilibrium becomes unstable, a limit cycle forms and the minimum prey density decreases rapidly with carrying capacity. The non-spatial model clearly shows the paradoxical consequence of enrichment of the environment (Rosenzweig 1971, May 1974).

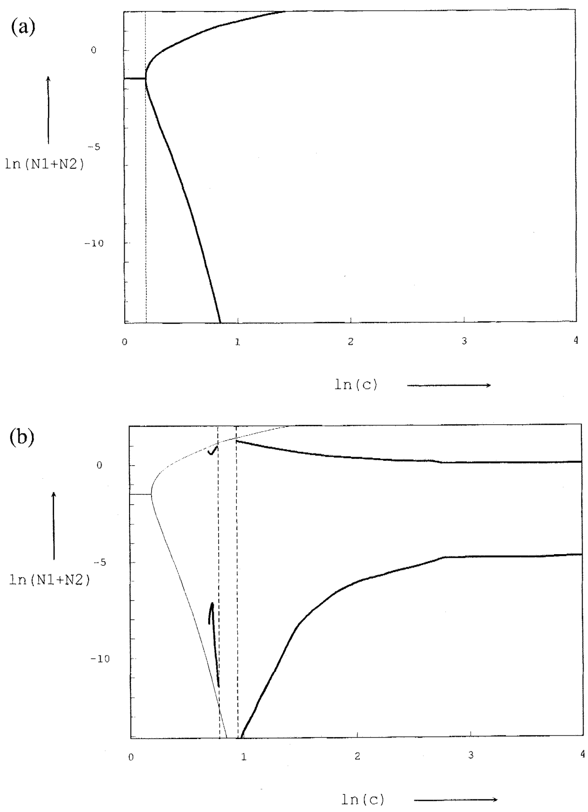

Fig. 4. (a) The minimum and maximum average prey density for the symmetrical attractors of system (2) versus carrying capacity. For carrying capacities on the left of the dashed line the attractor is an equilibrium, for carrying capacities on the right it is a stable limit cycle. For very large values of the carrying capacity logarithm of the minimum prey density is less than –15. (b) as (a) for all attractors of system (2). The thin line that is also depicted in (a) gives the minima and maxima over the symmetrical attractors. The thick lines give minima and maxima over non-symmetrical attractors. Between the dashed lines no non-symmetrical attactors were found. Non-symmetrical attractors on the far left and right are periodic, closer to the dashed lines the attractors are quasi periodic or chaotic. Parameter values: r = 1, $d_n = 0$, $d_p = 0.7$, $b = 9.96$, $\mu = 1$.

Fig. 4b shows the minima and maxima of the average prey density of all stable solutions of system (2). The symmetrical attractor is identical to the attractor in the non-spatial variant (Fig. 4a). Note that for the parameters used here the symmetrical solution keeps its stability for all carrying capacities. A non-symmetrical attractor (of the types shown in Fig. 3) can exist together with the stable symmetrical solution. For many initial values the final solutions will oscillate between two lines representing the non-symmetrical attractors. The minima of these initially decrease with carrying capacity. For higher values of the carrying capacity they increase and level out at a constant value. Although for certain parameter values very low prey densities are still possible, the minimal prey densities are bounded well away from zero for higher carrying capacities. Enrichment of the environment makes prey extinction less likely in spatial predator-prey systems and does not have the paradoxical consequences it has in the non-spatial analogue.

Discussion

Spatial models explain the dynamics of natural predator and prey populations better than their non-spatial counterparts. The region in parameter space where spatial predator-models have solutions which oscillate without reaching extremely low values is larger than it is with non-spatial models. Since they are based on an identical description of the local interaction this leads to the immediate conclusion that spatial interactions can be an important factor in the regulation of predator and prey populations.

None of the processes in the spatial Lotka-Volterra model with environmental noise can be classified as being density dependent, yet the densities do not easily reach extremely low values. For the spatial classical predator-prey model (2) something similar holds: an increase in the carrying capacity (this amounts to less density dependence since the prey equilibrium density is set by the predators) can result in smaller amplitude oscillations and thus stronger regulation. Migration as described in the models in this paper is a density independent process since all individuals have a constant per capita probability of leaving a patch, yet it can lead to a regulation of the population numbers. Many ecologists have tried to explain the regulation of predator and prey populations by identifying density dependent processes. The models presented here suggest that this approach need not be valid and that spatial interactions, based on density independent processes, can be the main mechanism through which these populations are regulated.

Admittedly, drawing these conclusions from a model where the spatial component is reduced to just two identical patches is somewhat tentative. However, more detailed and probably more realistic simulation models show that the spatial interactions can dominate the population dynamics of predator and prey (Hassell et al. 1991, De Roos et al. 1991, Wilson et al. 1993). Of particular relevance here are the studies by Hassell et al. (1991) and Comins *et al.* (1992). In their simulations they found different spatial patterns, depending on the migration parameters used. In a large parameter region they found spiral waves and related chaotic patterns that moved through space. In other parameter regions a fixed spatial pattern was formed. In these simulations the probability of the populations getting extinct drops quite rapidly with an increase in the number of compartments. It can therefore be expected that for the models presented here the parameter regions in which dynamics are dominated by the spatial interactions will expand rather than contract with a finer discretisation.

No matter how convincing these predictions can look, what ultimately is needed is an empirical test of these hypotheses. Although I do not know of any experimental results that show that predator-prey systems are more persistent in a spatially more complex environment, there are indications that they are. Firstly, natural populations normally do persist where many predator-prey systems are difficult to keep in the laboratory (Huffaker 1958, Huffaker et al. 1963). Secondly, acarine predator-prey systems can persist in greenhouses and show repeated oscillations (Nachman 1991). These oscillations can have a large amplitude if the local populations fluctuate synchronously, or oscillate with a reduced amplitude if the local populations fluctuate asynchronously (Van de Klashorst et al. 1992). In itself this is not very surprising since this is what one would expect to happen on grounds of simple statistics alone. The striking thing is though, that the asynchronous fluctuations can follow a period of synchronous fluctuations. Apparently the system has two different states it can be in and it can flip between those. This qualitatively resembles some of the dynamics produced by the models in this paper.

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